TOLERANCE OF FRESH WATER BY MARINE PLANTS AND ITS RELATION TO ADAPTATION

W. J. V. OSTERHOUT

Some effects of distilled water on protoplasm have been described by the writer.[1] Further investigations on this subject have shown remarkable differences between marine plants, and even between different cells of the same plant, with respect to their tolerance of fresh water. These differences are interesting from a physico-chemical standpoint, and significant because of their bearing on the theory of adaptation.

It is commonly supposed that most marine plants are killed by exposure to fresh water.[2] Some instances have recently come under the writer's observation in which death occurs with great rapidity. A good example of this is furnished by *Polysiphonia violacea*. Upon placing it in pure distilled water, many of the cells are killed within a minute. This is clearly shown by the fact that if they are replaced in sea water at the end of a minute they become disorganized and never recover. This effect of distilled water is not due to the presence of toxic substances acquired during distillation, for the water was prepared with especial precautions and was not toxic to sensitive species of *Spirogyra* and to sensitive root hairs. Moreover, the same effect is produced by water taken directly from ponds, rivers, and springs.

On the other hand, there are species which are quite tolerant of fresh water. Some years ago the writer[3] found marine algae growing along the sides of a steamboat. These were exposed alternately for some hours each day to salt water and to fresh water. They were also exposed daily to concentrated sea water and to strong sunlight, under which they reached a relatively high temperature. They included representatives of the red, brown, green, and blue-green algae, and were associated with a somewhat varied

[1] BOT. GAZ. **55**:446. 1913.

[2] Cf. PFEFFER, Pflanzenphysiologie **1**:415.

[3] Univ. Calif. Publ. Botany **2**:227. 1906.

fauna. One who is inclined to attribute this remarkable tolerance of fluctuations in salinity to a process of gradual adaptation will meet with many difficulties.

The writer recently had an opportunity, on the island of Mount Desert, Maine, to observe plants which are subjected to both fresh and salt water. At the mouths of brooks, in situations between tide marks which are exposed alternately to 6 hours of fresh water and to 6 hours of salt water,[4] there flourishes a surprisingly large flora, including representatives of the red, brown, green, and blue-green algae, and a flowering plant, the eel grass (*Zostera marina*).[5]

In some places tide pools are found in the beds of brooks. When the tide is out these pools are filled with salt water except for a layer of fresh water which rests on the top of the salt water and flows in a gentle current over it. The depth of the fresh water may be as much as 7 inches, and that of the salt water 2 or 3 feet. The line between the two layers is sharply marked.[6] In such places one portion of a plant may be exposed for several hours a day to fresh water, while the remaining portion is always in salt water. There seemed to be no differences between these portions of the plant.

What enables these plants to survive under such unusual circumstances? The current explanation is that they have gradually adapted themselves to these conditions. The eel grass might be

[4] As soon as the plants are covered with salt water by the rising tide, the fresh water no longer affects them, since it flows over the surface of the salt water without mingling much with it.

[5] Among the species which endure 6 hours of fresh water alternating with 6 hours of salt water may be mentioned the following, which were kindly identified by Dr. W. G. FARLOW: *Gomontia* sp., *Enteromorpha intestinalis*, *Monostroma Blyti*, *Fucus vesiculosus*. Some of these species, for example *E. intestinalis* and *M. Blyti*, endure much greater exposure to fresh water. Mr. F. S. COLLINS has noted that *Ilea fulvescens* (Rhodora **5**:175 and **6**:20; also Green algae of N.A., p. 206), *Enteromorpha micrococca* (Torr. Bull. **18**:336; also Green algae of N.A., p. 204), and *Pilinia minor* (Green algae of N.A., p. 292) stand exposure to fresh water. See also PFEFFER, Pflanzen-physiologie **1**:415 and OLTMANNS, Morph. u. Biol. der Algen **2**:173–183. 1905.

[6] Small animals in these pools (*Gammarus*, young eels, etc.) swim back and forth from one layer to the other without any sign of inconvenience. The boundary between the two layers is easily made visible by stirring; water-logged vegetable matter taken from the bottom of a fresh-water pool sinks to the boundary and remains there.

cited as an especially good example; its leaves are exposed alternately to fresh and salt water, but its roots, being covered by mud, are exposed to comparatively little change in salinity. The theory of adaptation might lead us to expect that the leaves of such plants would be much more tolerant of fresh water than the roots. This expectation is most strikingly confirmed by experiments, which show that the root cells of these plants are killed by fresh water in a few minutes, while the leaf cells can stand exposure to fresh water for several hours. But the argument must be reversed as soon as we make experiments with specimens of eel grass taken from salt water in places remote from the mouths of streams, where no opportunity for adaptation to fresh water occurs. In these plants we find the same differences between root and leaf with respect to their ability to withstand fresh water that we find in plants growing at the mouths of streams.

We must suppose, therefore, that characters which seem to be the result of adaptation were in this case present from the beginning and must be ascribed to entirely different causes. Doubtless this is also true of many cases which at present serve as typical instances of adaptation.[7]

There is much significance in the fact that leaf cells may withstand a much longer exposure to fresh water than the root cells of the same plant. One might be inclined to explain this by differences in the cell wall rather than by differences in the protoplasm, particularly as the cell wall in the root is usually more permeable to water than the cell wall in the leaf. It is clear that this is not the case here, however, for when leaf cells and root cells are placed side by side in hypertonic sea water, they are plasmolyzed with equal rapidity, and when replaced in ordinary sea water they recover at the same rate; this shows that their permeability to water and to the salts in the sea water is about the same in both cases.

Another consideration shows that the difference in the behavior of the cells cannot be due to differences in their permeability to water. This is the fact that death is not primarily due to absorp-

[7] Experiments with other species growing at the mouths of brooks showed that individuals which have had no opportunity for adaptation to fresh water show a great tolerance of it.

tion of water. In the process of dying the majority of cells exhibit little or no increase in size, showing that they absorb little or no water. Certain exceptional cells may swell and even burst, but this is not the rule.[8] Moreover, the cells die in isotonic cane-sugar solutions, although not as rapidly as in distilled water.[9]

We must look, therefore, for another explanation of these effects. It has been pointed out by LOEB that when death occurs in distilled water it must be due to diffusion from the protoplasm of substances which are necessary to its normal activity, and that doubtless the most important of these are inorganic salts. The reason why some protoplasm is more tolerant of distilled water may be that it parts less readily with certain salts which are combined (chemically or mechanically) with it.

It may also be true that the less tolerant protoplasm consists more largely of substances (globulins or other colloids) which undergo a change of state as soon as the concentration of salts falls below a certain limit. In order that the cell should be intolerant of distilled water the globulin (or other substance) need not constitute a large part of the protoplasm, for it might, even in small quantity, play an extremely important rôle, such as that of a protective colloid or of a constituent of the plasma members. These effects would be very simply explained by such an assumption.

LABORATORY OF PLANT PHYSIOLOGY
HARVARD UNIVERSITY

[8] In some cases failure to swell may be due to the rigidity of the cell wall, but certain cells which have no rigid cell wall fail to swell under these conditions.

[9] This has been shown for certain animal cells by LOEB, Pfluger's Archiv **97**:406. 1903.